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Phenological resonance and quantum life history

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Abstract

The principle of 'quantum life history' is proposed here as a complementary viewpoint to current modeling of body size and life history evolution which usually considers a 'fast–slow continuum' of covarying life history traits. This principle emphasizes the discrete (and primary) nature of development time caused by the effect of phenological resonance (the compliance of development time with periodicities of earth rotation). The body mass, in turn, complies with development time, which generates body mass attractors. This principle is illustrated with mammals as exemplary group. The adaptive radiation of Cenozoic mammals is supposed to proceed as a competition-driven diversification of body sizes and development times around the strongest (year-long) resonant mode of development time corresponding to body mass of about 1 kg. Mammals with this body mass are shown here to have a largest genome size and a lowest (body mass-corrected) basal metabolic rate. This extends the previously reported negative relation between genome size and metabolic rate to the realm of nonlinearity, and suggests that selection against the accumulation of non-coding DNA in the genome is relaxed in mammals with this body mass.

Keywords: Body mass; Development time; Genome size; Metabolic rate; Optimality; Mammals

1. Introduction

It is well-known that many life history traits are closely correlated, body size being a main determinant for majority of them. The space of covarying life history traits is usually considered as a 'fast–slow continuum' (e.g. Purvis and Harvey, 1997; Ricklefs and Wikelski, 2002). Here we demonstrate the opposite feature of this space—its discontinuous nature caused by a metronome of earth rotation.

It is reasonable to suggest that compliance with phenological changes plays a great role in the organism's life history, especially in the development. The importance of such 'phenological resonance' can be appreciated from the sharp peaks of frequencies of mammal development times that correspond to parameters of earth rotation (Fig. 1). The sharpness of this picture is unusual for biology and is strikingly resembling the quantum spectra of light emission caused by resonant atomic modes. The distribution of body masses also complies with this principle of 'quantum life history'. The ridge on the bivariate histogram of development time—body mass regression is split into peaks (Fig. 2). The first peak corresponds to the season-long development, the second peak to the year-long, and the third, elongate peak represents the merged 2-year and longer development times. The peaks of body masses are smoothed as compared to peaks of development times (hence peaks with times above 1 year are merged). This indicates that it is the development time that is a primary cause of this discreteness. The smoothness of body-mass peaks is probably caused by ecological competition that repulses body masses from the optima corresponding to resonant development-time modes. Besides phenologically explainable peaks, there are small separate peaks formed by mammals whose body masses are affected by a shift in habitat medium (bats and whales) (Fig. 2).

As an example of explanatory power of this concept, we consider the puzzles from ecology and evolution, which are not understood with gradual models. It is known that mammals with mean body mass about 1 kg show the highest (body mass-corrected) population densities (Damuth, 1993). This body mass was already suggested to be optimal for mammals from phenological reasons because it corresponds to a year-long development time (Vinogradov, 1994). The body mass about

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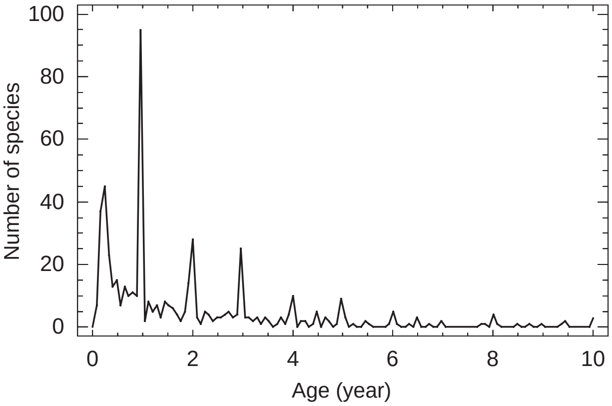

Fig. 1. The effect of phenological resonance seen on the histogram of development times in mammals. (Total 547 species, data set is from Wootton (1987). This author noted some aggregation of points in the regions of 1 and 2 year on the scatter plot of body mass vs. development time, but the effect cannot be properly appreciated from such plot.)

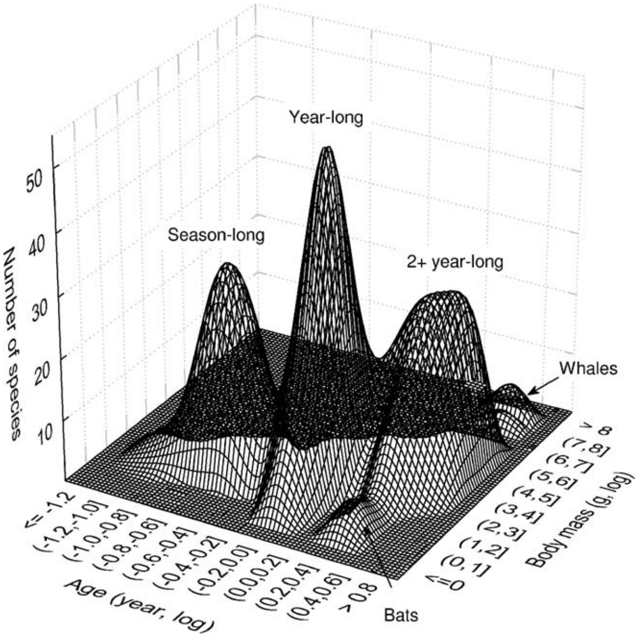

Fig. 2. The principle of quantum life history illustrated with the bivariate histogram of development time vs. body mass in mammals (peaks of development times serve as body mass attractors). (The same data set as in Fig. 1.)

100 g was also frequently featured as showing the highest population and species densities (Brown et al., 1993; Silva et al., 1997). A model was proposed that claimed the optimality of this body mass from consideration of foraging parameters ('BMT-model') (Brown et al., 1993). However, this model was criticized both on the theoretical ground and because it gave wrong predictions (Kozlowski, 1996; Chown and Gaston, 1997; Jones and Purvis, 1997; Symonds, 1999). The effect of phenological resonance with a local time-mass optimum corresponding to the season-long development suggests an obvious explanation for the increased frequency of mammals with such body mass (Fig. 2).

It is known that Cretaceous mammals were small (logarithmic mean below 100 g), then just around the Cretaceous–Tertiary (K–T) boundary there was an abrupt shift in the mean body mass which exceeded 600 g (Alroy, 1999). This rapid increase resulted from the extinction of small mammals and the appearance of medium-sized ones, i.e. it was the real shift, not just a diversification of sizes (on logarithmic scale, the range of body masses even decreased; the coefficient of variation dropped from 45% to 29%). In the first million years of the Cenozoic, the mammal species, above 80% of which were new, averaged 1 kg (Alroy, 1998). This extraordinary shift is unequalled elsewhere in the mammals evolution (Alroy, 1998). It is plausible that at the K–T boundary there was a transition between two resonant modes, i.e. from the season-long to the year-long development with the corresponding shift in mean body mass. The global cooling, general instability of climate and an abrupt change of other environmental conditions, which are known to occur at the K–T boundary (Corfield, 1994; Pope et al., 1997; Vajda et al., 2001), probably made it necessary for mammals to increase body mass and to tune up to a sharper phenological metronome of a year-long period as compared to a smoothed season-long one (Fig. 1). (An ecological release due to mass extinction of reptiles usually featured as a cause of this shift, taken alone, cannot explain the extinction of small mammals.) Thus, the adaptive radiation of Cenozoic mammals might have proceeded as a competition-driven diversification of body sizes and development times around the basic (year-long) resonant mode, which was arrived at just after the K–T transition. This diversification expanded to other, secondary resonant modes.

It is interesting that mammals with body mass about 1 kg have the largest genome size (Fig. 3). Even the raw polynomial regression of genome size on body mass shows a statistically significant nonlinearity (Fig. 3A), but the position of maximum is better seen in the polynomial approximation of residuals of linear regression (Fig. 3B). It is known that there is a negative relation between genome size and body mass-corrected basal metabolic rate in mammals (Vinogradov, 1995). This relationship is extended here to the realm of nonlinearity: mammals, which in polynomial approximation show the maximum residuals of genome size (Fig. 4A), have the minimum residuals of basal metabolic rate (Fig. 4B).

It is possible that purifying selection against the growth of genome through accumulation of non-coding DNA is relaxed in mammals with this body mass because of the optimality of this mass from the

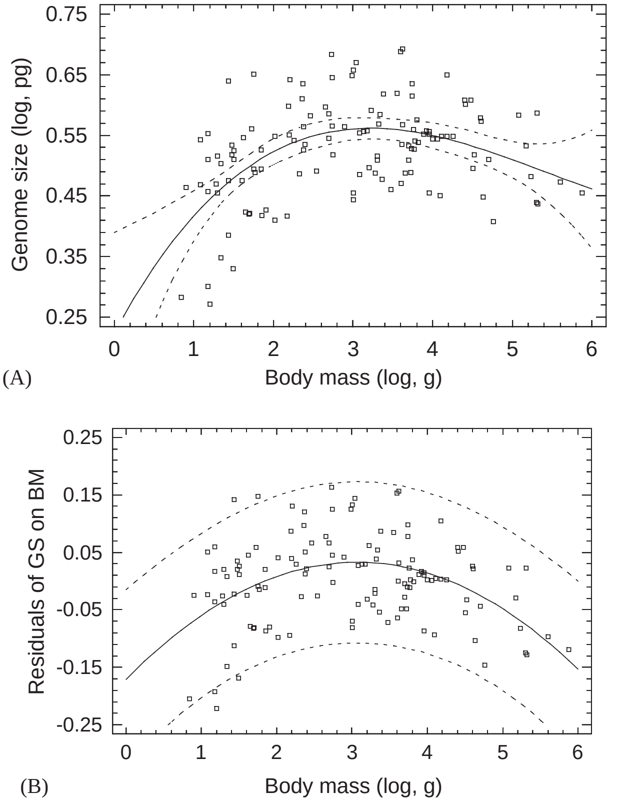

Fig. 3. The nonlinear relationship between genome size and body mass in mammals. (A) Polynomial regression of genome size on body mass. (B) Polynomial approximation of residuals of linear regression of genome size (GS) on body mass (BM) ($p < 10^{-4}$ for nonlinearity, i.e. for the second-order polynomial term). (Total 125 species, data on genome size are from Gregory, 2001, on body mass from Wootton, 1987.) Dotted lines, confidence limits (for $p = 0.95$).

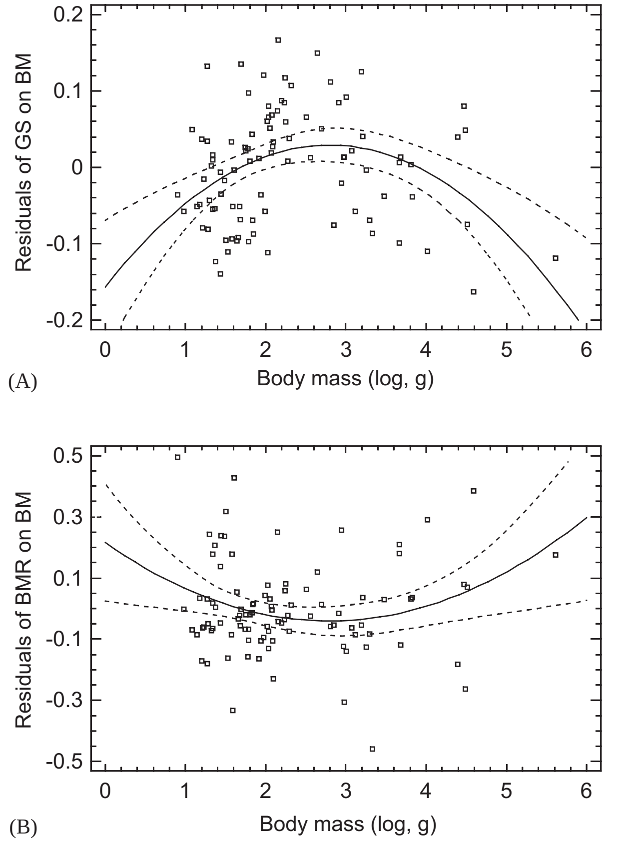

Fig. 4. The nonlinear relationship between genome size, body mass and basal metabolic rate in mammals. (A) Polynomial approximation of residuals of linear regression of genome size (GS) on body mass (BM) ($p < 10^{-3}$ for nonlinearity). (B) Polynomial approximation of residuals of linear regression of basal metabolic rate (BMR) on body mass (BM) ($p < 0.01$ for nonlinearity). (Total 95 species, data on genome size are from Gregory (2001), on body mass and basal metabolic rate from Lovegrove (2000). The BMR data set is biased in regards to smaller mammals as compared to the data set used in Fig. 3. Therefore the maximum of GS polynomial approximation is slightly shifted to the left as compared to Fig. 3B, but this shift is similar both for GS maximum and BMR minimum.) Dotted lines, confidence limits (for $p = 0.95$).

phenological and physiological reasons. It was a mean body mass when a general physiological design of modern mammals was formed in the early Tertiary before their adaptive radiation, and consequently, this design might have been optimized for it. This conclusion is supported by the data on somatic polyploidy, which show that workload on two organs considered to be bottlenecks of mammal design (heart and liver) is well balanced in mammals with body mass about 1 kg, whereas it is biased on one or another organ in mammals with significantly higher or lower body masses (Fig. 3B in Anatskaya and Vinogradov, 2004). From the standpoint of environment carrying capacity, the minimal metabolic rate of mammals with this body mass can be related to the fact that they show highest population densities (corrected for body mass). Because of the technical problems of comparison of genome sizes in groups with a low variation of genome size, such as mammals (Vinogradov, 1995, 1998), it cannot be expected that genome size distribution would form sharp peaks (corresponding to all resonant modes). More likely, only the main peak would appear (corresponding to 1 year-long mode, as in Fig. 3B), and possibly even merged with the season-long peak (when there are many small species in the data set, as in Fig. 4A).

The principle of quantum life history, which emphasizes the discrete (and primary) nature of development time and the compliance of body mass with it (which generates body mass attractors seen in Fig. 2), represents a complementary viewpoint to current modeling of body size and life history evolution, which usually considers gradual, continuous changes. It is quite probable that other phylogenetic groups also have discontinuous development time—body mass spectra, formed and tuned by earth rotation while smoothed by ecological competition. The strongest year-long resonant mode might have served as a center of adaptive radiation in different phylogenetic groups.

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